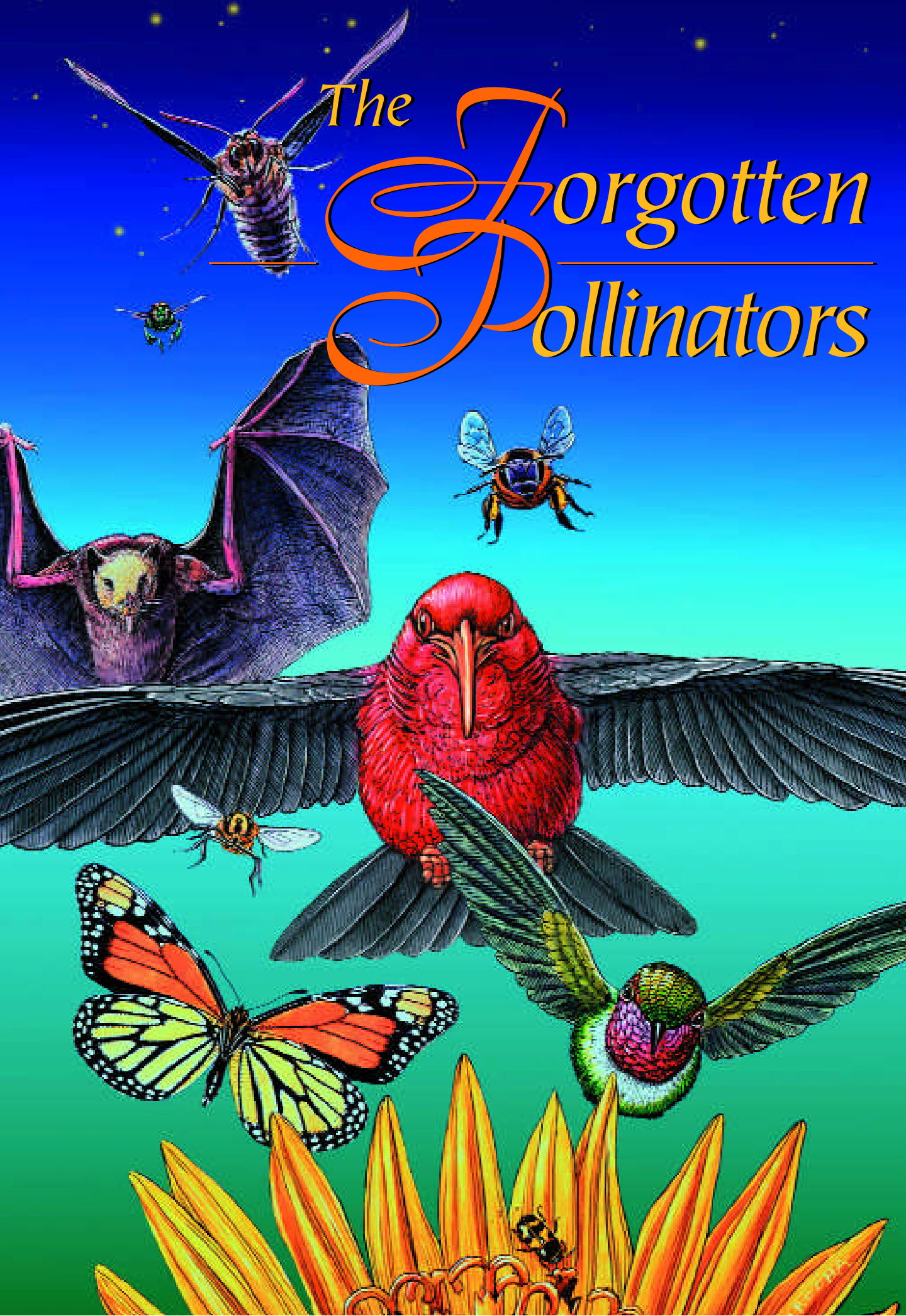


The
Forgotten
Pollinators



The *Forgotten* *Pollinators*

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*Forgotten Pollinators Campaign,
Arizona-Sonora Desert Museum*

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ISLAND PRESS / Shearwater Books
Washington D.C. / Covelo, California

A groggy male squash and gourd bee (Xenoglossa angustior) has just climbed out of its nocturnal roost in a zucchini squash blossom. Soon it will begin a daily quest in search of female bees of its species as they visit blossoms for nectar and pollen. Like many territorial male solitary bees, it is an important pollinator.



Holding the Globe in Our Hands

The Relentless Pressures on Plants and Pollinators

GARY REMEMBERS:

We passed the somewhat soggy, punctured, hard-shelled gourd back and forth between our hands, as if it were a miracle among us. For the first time in six years, the Okeechobee gourd had been found, still surviving somehow, in the Southeastern United States. With the help of an old friend, I had at last determined that *Cucurbita okeechobeensis* (subspecies *okeechobeensis*) was not yet extinct, though it was undoubtedly endangered within its wetland home.

Other naturalists had already given up hope that it would ever be seen in the wilds of Florida again, for it faced fierce threats on all fronts. The gourds were surrounded by exotic weeds—from moonvine to smartweed—that handily outcompeted most plants indigenous to this swamp of custard apples. The custard apple trellises, which had for decades served the climbing gourd vines, were now in decline as the Southern Florida Water Management District played god with the water levels in Lake Okeechobee, sequentially starving, then drowning out, the remaining custard apple trees. Nearby, former habitat had been drained and planted with sugarcane. Where mosquitoes bred in the pools of irrigation tailwaters, aerial spraying kept both pests and beneficial insects in check. Even in “protected” wildlife areas in southern Florida, such spraying has been found to affect nontarget insects for distances up to 750 yards.

Long after I stood waist-deep in those alligator-infested swamp waters, I realized there was one beneficial insect that should have been buzzing around that custard swamp but has never been found there. Among entomologists, this big orange and brown native bee goes by the name of *Xenoglossa strenua*. This solitary bee has been found nearly everywhere squashes, pumpkins, and gourds have been grown in the southern United States and adjacent subtropical Mexico. If the gourd had been there for

centuries on the shores of Lake Okeechobee, as I suspect it has, then this big mahogany-colored bee should have been there as well. In all the Americas where gourd blossoms have flowered since prehistoric times, there is simply no place that lacks this bee or its close relatives. In fact, squash and gourd bees are found in abundance on the Florida gourd's closest kin, the subspecies known as the Martinez gourd, wherever it grows on the Caribbean coast of Mexico. Why not here?

It has been ten years since the Okeechobee gourd was rediscovered on an island in the lake, but the full puzzle has not yet been put together. Recently, though, entomologist Mark Minno of Gainesville, Florida, rediscovered a second population of Okeechobee gourds within a mile or two of where naturalist John Bartram first described this species in 1774. There, in swamps along the St. John's River near Lake Dexter, Florida, Bartram observed "a species of *Cucurbita* which spread and ran over bushes & trees 20 or 30 yards high [and] which reflects on the still surface of the River a very rich and Gay picture." Mark Minno was much more matter-of-fact about his own discovery: "We just happened to be out there one day, and happened to see these gourds out in the swamps, and thought they might belong to the Okeechobee gourd species. We were just astounded that no one had really looked for it there since Bartram's time."

Minno did not have the luxury of floating a river as placid as that which Bartram describes: he found the gourd in high floodwaters while wading up to his armpits in another swamp inhabited by alligators. While his training in entomology allowed him to spot some melonworms—larvae of pyralid moths—feeding on the vines, he has yet to see solitary bees among the vines, despite his periodic return to monitor the gourds. There is fruit set due to honeybee pollination. Other biologists now intensively working with the Lake Okeechobee population of the gourds also report fruit set, but they too have yet to report any of the native bees.

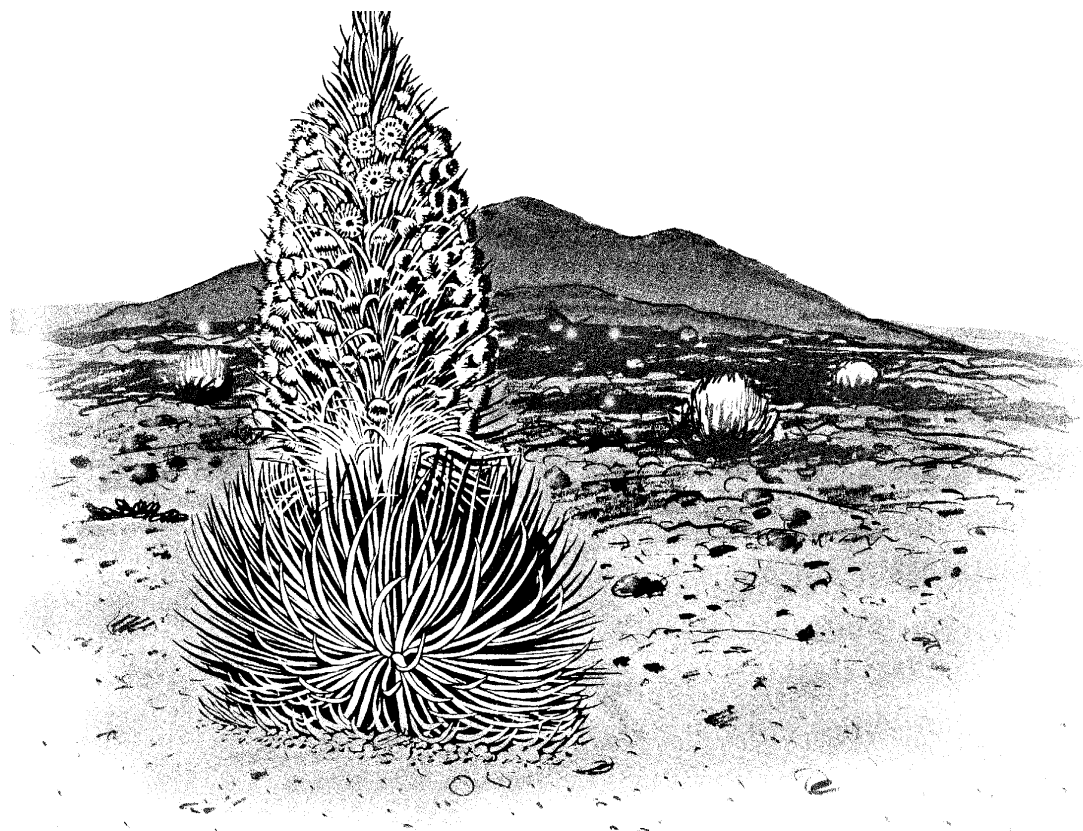
A lack of reports, in and of itself, does not necessarily mean that the squash and gourd bee was once there but is now extinct. It is symptomatic, though, of a larger problem—that of missing information relating to the animal associates of some of the rarest plants in the world. As Peter Kevan of Guelph University in Ontario once pointed out, the information available on pollinators' interactions with plants is often the weakest link in our chain of understanding how ecosystems function.

In 1989, the Okeechobee gourd was listed among some 250 plants that the Center for Plant Conservation predicted would go extinct in the wild within ten years. Even if it continues to be grown in botanical gardens, there is a high likelihood that it will become functionally extinct in its natural habitat. It is without the animals that have been associated with wild gourds over the millennia—merely a "living Latin binomial" as ecologists Robert May and Anne Marie Lyles have called captive-bred species that are deprived of their original ecological contexts.

Filling such an ecological void can be difficult, as William Stolzenburg of The Nature Conservancy has documented for two Hawaiian species of *Brighamia*. The two rosette-forming plants are collectively known from barely more than 120 individuals left in the wilds of Molokai and Kauai. They rarely set seed any more unless they are hand-pollinated by what Stolzenburg describes as the "death-defying acrobatics of human moths." The human moths, in this case, are biologists from the Hawaiian Plant Conservation Center who rappel over the brink of 3,000-foot precipices above the sea. Then, hanging from ropes, they brush precollected *Brighamia* pollen onto the stigmas of the few trumpet-shaped flowers growing out from the world's tallest sea cliffs.

These biologist-acrobats are trying to play the role once played by the native pollinators that *Brighamia rockii* and *B. insignis* have lost over the last two centuries. Today, only half of Hawaii's original set of nectar specialists persist—and many of the remaining nectar-feeding birds, from the Hawaiian *alala* crow to the crested *ākohekohe* honeycreeper, are officially listed as threatened

Atop the Haleakala volcano in the Hawaiian Islands grows the “ahinahina” silversword (*Argyroxiphium sandwicense*)—an example of gigantism among a group of plants we normally pull out of our lawns as dandelions. These plants are now threatened and can no longer depend on a stable pollinator population, or enough nearby plants, for their reproduction.



or endangered. Stolzenberg reminds us that the idea of *linked extinctions* suggests that one species’ demise is triggered by that of its evolutionary partners. “If ever there might have been a stage set for exhibiting linked extinctions,” he concludes, “Hawaii was it.”

Stolzenberg may be correct in bestowing this dubious distinction on the Hawaiian Islands, but others might argue that Madagascar is just as vulnerable to linked extinctions. The Malagasy Republic on the island of Madagascar ranks among the top five countries in the world in terms of *endemism*—the percentage of its total species found there and nowhere else. Roughly 54 percent of its butterflies, 95 percent of its reptiles, 46 percent of its birds, 41 percent of its bats, all of its primates, and all of its thousand or so orchids are unique to the island. By the 1990s only 10 percent of Madagascar’s original forest cover remained intact and less than 2 percent of its land base had achieved nominal protection. Deforestation, agricultural conversion, hunting, and overcollecting in the Malagasy Republic have depleted populations of one animal after another. According to the IUCN, 18 primates, 28 birds, 110 reptiles, 22 amphibians, 15 fish, and 45 butterflies native to Madagascar have suffered severe declines in recent decades.

If University of California conservation biologist Harold Koopowitz is correct, even these dismal numbers underestimate the severe loss of biological diversity from Madagascar.

Koopowitz has developed a model that predicts the number of species extinctions. His model is based on the probability that random deforestation of various localities affects plant species known only from a few sites more than it affects widespread species. Unfortunately, 87 percent of Madagascar's well-studied orchid flora are restricted to three sites or fewer. Using an extremely conservative estimate that two-thirds of the island's forest cover has already been lost or damaged past its capacity to support orchids, Koopowitz predicts that over 500 orchid species must already have disappeared from Madagascar. If deforestation has left only 10 percent of Madagascar's natural vegetation sufficiently intact to support viable populations of orchids, the minimum loss already suffered is closer to 747 species. Koopowitz warns that these estimates allow "orchid survival" to be defined in the most minimal terms—that is, as single plants still persisting in a habitat. But many orchids are obligate outcrossers, and one individual is not enough to keep a population or species viable over any period of time. Koopowitz concedes that such minimally persisting species will probably die out, not because of random events, "but rather because of demographic problems that lead to inbreeding depression or inability to achieve pollination."

L. Anders Nilsson and his Malagasy colleagues have provided on-the-ground verification of the trends the Koopowitz model predicts with regard to orchid pollination in forest fragments. Nilsson focused on the *Cynorkis uniflora* orchid, which produces nectar in a floral spur that is accessible only to hawkmoths with very long tongues. In disrupted fragments of hilltop forests, the hawkmoth fauna available to orchids has become skewed—in fact, many more nectar thieves than legitimate long-tongued pollinators are represented. This imbalance has changed the degree of genetic variation in the remnant orchid populations, for long-tongued hawkmoth pollinators now draw upon relatively few plants for pollen. And the bulk of the orchid seeds produced are sired by a small number of pollen donors, indicating reduced genetic diversity. Nilsson is prophetic in his interpretation of these disruptions: "Interhabitat ecological links between larval host-plants, adult insects, nectar thieves and pollination are probably critical components in most pollination systems in the tropics. Destruction of forest habitats will inevitably cause more or less severe imbalances among pollinating guilds of animals across habitats, and interactions may become extinct prior to the organisms themselves."

In a more recent assessment, Koopowitz and his colleagues have broadened their concern from the fate of the orchids alone to their pollinators and seed dispersers: "In the real world, deforestation is probably hardly ever complete, and some individuals can be expected to survive the ax or the plow. Some plants can endure for extended periods of time under adverse conditions, but whether their pollinators and other commensals can also persist so that reproduction can continue appears unlikely."

Although the Koopowitz model was first applied to Madagascar, it has also been used to predict the fate of the neotropical floras of South and Central America. Five of the world's fourteen megadiversity countries—Brazil, Mexico, Colombia, Ecuador, and Peru—are located in this neotropical region. There 19 percent of the original forested area has been cleared since 1950. On the basis of locality data from 4,258 species in the neotropical flora, Koopowitz, Thornhill, and Andersen have predicted that 3,020 plant species formerly known from three sites or fewer have already been lost since midcentury. If current deforestation rates continue unabated, the entire neotropics may lose 70 to 95 additional plant species every year.

Let's see what the model suggests for just one country known for its megadiversity, Ecuador. Ecuador ranks in the top ten countries in the world in terms of species richness and endemism. One-eighth of its 1,120 butterflies are found only within its boundaries—giving Ecuador the third-richest lepidopteran fauna in the world. In addition, Ecuador may have been home to as many as 20,000 plant species earlier in this century. But Ecuador is also in the top ten countries in the world with regard to its rate of forest loss. At least 54 percent of the Ecuadorian forests standing in 1950

have been lost due to lumbering, agricultural conversion, and oil exploration. The Koopowitz model suggests that Ecuador may already have lost 3,275 plant species since 1950, or 16 percent of its flora. And given current rates of the country's deforestation, another 67 flowering plants are annually being driven toward extinction.

Orchids comprise a significant portion of these losses. For pleurothallid (side-shooted) orchids, which have their center of diversity in Ecuador, 402 of the 3,405 known species may have already been driven to extinction by deforestation. In Ecuador and adjacent nations, deforestation is contributing to the loss of one *Masdevallia* orchid every year and one *Dracula* species every three years.

Koopowitz, Nillson, and others emphasize the plight of orchids for two reasons. First, orchids comprise perhaps one out of every ten flowering plants on the planet. Second, orchids are often epiphytic—they grow upon other plants—and thus are extremely vulnerable in areas where trees are felled. Deforestation since 1950 may have already wiped out 22 percent of the 25,000 orchids that have been described by botanists. Simply put: by the year 2000, about one-fourth of the world's largest plant family may be wiped out as the result of the last half century of deforestation and land conversion in the New World and Old World tropical forests.

Earlier we noted that most of the so-called orchid bees do not have strict one-on-one mutualistic relationships with orchid species. Nevertheless, many of these bees will surely be affected by deforestation's toll on orchid diversity. Let us assume—along with euglossine bee expert Dave Roubik—that one-half to three-fourths of all euglossines in the neotropics visit orchids with some frequency. Overall, orchid bee species may number from as little as 5 to as many as 50 per site, with 15 to 30 active in any particular month. Based on their surveys in central Panama, Roubik and his colleague James Ackerman have recorded 38 euglossine bees frequently visiting 51 orchids. (Another 19 bees visit them rarely or never. As many as 24 orchids can be found at a single site.) Because 36 of the 38 bees were found at multiple sites, they would not necessarily be driven to extinction should a single site be destroyed—as 11 of the orchids themselves might be. But 29 of the bees visited only one orchid species and thus would be particularly vulnerable should that orchid die out at all sites.

Roubik and Ackerman do not necessarily see the coevolution of orchids and euglossine bees as being so equally weighted that a bee would be lost for every orchid lost:

Orchids are clearly dependent upon euglossine bees for pollinator service, and much specialization may have occurred via adaptation to specific pollinator pools. [While there is] no evidence that euglossines [exclusively] are dependent on orchids for volatile chemicals . . . species that did not carry pollinia [from orchids] were not abundant. These data imply specialized dependency and perhaps indicate that bee species cannot become abundant if they lack orchid hosts.

If over a third (37.9 percent) of all orchids are known from just one locality, and over two-thirds (68.2 percent) are found in three localities or less, deforestation will take its toll on many geographically restricted orchids and the orchid bees dependent on them. If a bee has even a partial dependence on a particular orchid species, chances are slim that it will find other nearby sites where the orchid might still exist. Unless it can switch to another, more generalized orchid to obtain the fragrances, pollinia, or nectar it requires, the bee will surely be faced with extinction.

To make matters worse, wholesale habitat clearing is not the only threat to plants and pollinators in the world's megadiversity countries such as Ecuador and Madagascar. Although many of the 26,000 plants in the world that are threatened with extinction are vulnerable to chainsaws, bulldozers, and plows, their habitats can also be degraded or fragmented in more subtle ways. Forests may be degraded without being clear-cut and the results can be just as devastating. In the

Lomas Barbudal dry forest of Costa Rica, biologists studied bee diversity in intact forests and then returned 15 years later to find that the same site had survived clear-cutting but not fragmentation. They demonstrated that solitary bee diversity there declined due to a variety of factors: the loss of fragrant oils required for reproduction by male bees, the loss of female nesting sites, the impact of fires on nesting success, and the loss of nectar sources critical to the development of young bees. The average number of solitary bees per sweep, on the same day of the year at the same locality, declined from 70 bees in 1975 to 37 in 1989.

Such dramatic short-term declines in species composition are surprising, because most models predict a 50 to 400-year time lag before habitat fragmentation results in extirpations or extinctions. And yet these same models warn us that eventually we may not simply lose rare species, but some of the more dominant ones as well: the species that exert major control over ecosystem functions, as well as the species that are the most efficient pollinators of the world's flowering plants.

We are disturbed by the implications of one such model, developed by David Tilman of the University of Minnesota, along with Robert May and others at Oxford University. Their model of habitat fragmentation attempts to predict the extinction debt our generation is passing along to other generations—and when this debt will come due in the future. They have verified that even a slight increase in habitat fragmentation threatens many species, particularly in places where a large portion of a habitat has already been fragmented. Their model compares the consequences of added habitat destruction in cases where 20 percent of a region's vegetation has been destroyed. If you increase the rate of habitat destruction in that region by just 1 percent, extinction rates then become eight times higher if 90 percent of the native plant cover is already gone than if only 20 percent of the protective plant cover has been cleared away.

And yet Tilman and his colleagues warn us there are large differences in how habitat fragmentation plays out in tropical versus temperate forests. In one of their model simulation scenarios, destruction of just one-third of a tropical rainforest triggered the extinction of 35 percent of the total species in the area. Most of these extinctions did not occur immediately, but took up to 400 simulated years after the habitat became dramatically fragmented. In contrast, the same magnitude of destruction eliminated only 5 percent of the total species in a temperate forest—but those extinctions occurred within 40 to 60 years after habitat fragmentation. In general, the smaller, more abundant species (such as insect pollinators) gradually declined in the modeled temperate forests, while large vertebrates and other rare species were much more quickly affected by habitat loss in the tropical rainforests.

Habitat fragmentation also increases pollinators' exposure to invasive competitors, to parasites and diseases, and to pesticides. The Pesticide Trust and other organizations have raised their concerns about the effects of uncontrolled pesticide and herbicide use in five of the fourteen countries richest in biological diversity: Ecuador, India, Brazil, Malaysia, and Mexico. People and animals in these countries must face the heightened exposure to herbicides and insecticides that often accompanies forest clearing and wetland drainage to open lands for farming and ranching. In Ecuador, for example, one-fifth of the 6,200 tons of pesticides imported in 1990 comprised chemicals that cause reproductive abnormalities in humans and other animals: paraquat, carbofuran, dichlorvos, endosulfan, methamidophos, methomyl, monocrotophos, and phosphamidon. Pesticide sales to Ecuadorian farmers have more than doubled since 1980. And yet, as one Ecuadorian agronomist (who asked to remain anonymous) has confirmed, pesticide applications are seldom controlled sufficiently to reduce exposure to humans, beneficial insects, or other animals: "Selling pesticides to farmers in the way it is done in Ecuador is like giving strychnine to people who don't know what it is."

Similar reports have recently come out of Mexico, which dramatically increased its pesticide imports following the North American Free Trade Agreement (NAFTA). According to one

Mexican official, more than 165 million pounds of pesticides were used in the country in 1993—and in the first six months after NAFTA went into full effect, pesticide imports jumped another 50 percent. Mexico had already experienced a decade and a half of escalating sales of pesticides, however, from \$199 million worth in 1980 to well over \$560 million in 1990. Mexican farmworkers are now spraying a number of highly regulated or banned chemicals known to poison bees and other pollinators: aldrin, carbaryl, chlordane, DDT, dieldrin, endrin, heptachlor, malathion, and parathion. Twelve of the chemicals currently being used in northern Mexico are known to disrupt the endocrine systems of animals, including many pollinators, no doubt resulting in long-term declines in reproductive success among some species. In terms of their lethal dose toxicity for bees, all insecticides are not created equal. DDT is moderately poisonous to honeybees and for solitary bees, while highly toxic killers include such formulations as malathion.

There is considerable irony in the fact that Mexico is importing such large quantities of hazardous chemicals from the United States and Canada as part of NAFTA—for Mexico is home to many more native pollinators than occur in either of the other two North American nations. Consider the butterfly as an indicator of pollinator diversity. Mexico is home to 471 species of butterflies, 46 of them endemics; Canada has less than a third that number, with 150 species, only 2 of them endemics; and the United States hosts 292 species, only 22 of them unique. Essentially, all of the approximately 160 genera of bees known from the North American continent can be found in Mexico.

Brazil is a country of perhaps even greater concern, for it ranks third in the world in plant and animal endemism and fourth among all countries in species richness. Although its rate of forest loss is ranked “only” sixth among the nations of the world, this conversion of forests is clearly being followed by the intensive use of agrochemicals that potentially affect many pollinators. Brazil is both the major user and the major producer of pesticides in Latin America. Its farmers spent \$2 billion on them in 1990—half as much again as all other users in the region combined. Brazilian pesticide sales have nearly tripled since 1980, so that nearly 5 pounds of pesticides are annually used by each of the 23 million farmworkers in the country. These chemicals are used to control mosquitoes, cotton pests, agricultural weeds in newly opened fields within fragmented forests, and roadside weeds. One Brazilian toxicologist has estimated that 280,000 Brazilians—an incredible 2 percent of the total population—are poisoned by pesticides each year. If humans are exposed in such quantities, it is almost too frightening to imagine the intensity of exposure of target and nontarget invertebrates. The severity of pollinator declines resulting from this insidious connection between land clearing and deadly chemicals is not likely to be known for decades. But there is no doubt that the rainforest is being cut down equally effectively by both metal and “chemical chainsaws.”

When James Przeslawski recently interviewed Amazonian orchid expert Callaway Dodson, he realized that Latin America is quickly coming to the end of the never-ending forest. In Dodson’s words:

The old saying in Ecuador is “Fat parrots mean skinny children.” When it’s thrown at you that way, what do you do? The last two decades of destruction have been the result of overpopulation in which the government has sought to take the pressures off the cities by giving forests to colonists. The end result has been deforestation at an almost unbelievable rate; you can’t believe how fast it is vanishing. And it’s not slowing down; it’s accelerating as the next generation comes into their reproductive agespan. If the reproduction stays that high, then there appears to be no hope. The parrots have had it. They’re on their way out and so are the orchids!

Massive forests are being reduced to piecemeal fragments on other continents as well. We may someday see on the large landmasses of this planet what we already see on islands: once-common

plants, formerly capable of attracting a diverse assemblage of pollinators, becoming limited to only one generalist pollinating species, such as the European honeybee, so common in many secondary patchwork habitats.

If one plant has a prophetic message for us, it is the kapok tree, the Mayan tree of life. Within the intact forests found on various continents, naturalists have recorded that giant kapok trees are actively pollinated by insects, perching birds, opossums, primates, bats, and hovering birds. Within an island population of kapoks in Western Samoa, however, only one animal pollinator is available to move pollen from one tree to the next for this obligate outcrosser: the flying fox, *Pteropus tonganus*. Flying foxes are in decline throughout the South Pacific. Should this species become overhunted or find its habitat deforested, the only pollinator for the kapoks on these islands may disappear. Tom Elmqvist, Paul Cox, and colleagues have put it this way: “Flying foxes are critical pollinators for forest plants on isolated oceanic islands where the pollinator fauna is depauperate. . . . The loss of flying foxes would have serious consequences for the long term viability of isolated island ecosystems.”

This finding echoes a concern raised by many biologists—from the Smithsonian’s Tom Lovejoy to Harvard’s Edward O. Wilson and *Outside’s* David Quammen. The point is becoming clear: Oceanic islands are no longer the most isolated ecosystems on this planet; some forest fragments now show the very same syndrome. These fragments can be thought of as islands awash in a terrestrial sea now stripped of many keystone mutualists including pollinating animals. No doubt we will begin to see depauperate pollinator faunas evident in forest remnants, physically and chemically denuded habitat fragments, on each of the naturally vegetated continents. As underscored earlier, fewer “islands” these days are tropical paradises for pollinators, and nothing about forest, prairie, or desert patches in seas of degraded landscapes will remind us of a bygone once-pollinated and fruitful Eden.